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Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar

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This paper examines bat-plant interactions by focusing on the fruit diet and food selection of flying foxes (*Pteropus rufus*) in the littoral forest fragments of Sainte Luce, SE Madagascar. Analyses of faecal samples and opportunistic observations revealed 40 endemic plant species in the diet. The bats mainly eat odorous ripe and juicy berries. No particular fruit colour was predominant in their diet. Both multi- and single-seeded fruits are eaten. Small seeds (1–3.5 mm in length) are usually swallowed whole. Passage through the digestive tract of the flying foxes does not reduce the germination rate of seeds nor the percentage of seeds germinated. This study indicates that the role of flying foxes in both short and long distance seed dispersal for a large number of endemic tree species of the littoral forest should not be underestimated when designing reforestation programs in particular or conservation action plans in general.

Key words: *Pteropus rufus*, seed dispersal, frugivory, Madagascar

INTRODUCTION

Pteropus rufus is an endemic flying fox in Madagascar and belongs to the Old World family Pteropodidae (Megachiroptera). The genus *Pteropus* lives mainly on islands (Cheke and Dahl, 1981; Banack, 1998). Its representatives are almost entirely frugivorous, feeding mostly on fruit pulp, juices, nectar, and occasionally also on leaves (Marshall, 1983). *Pteropus rufus* occurs predominantly in the humid forests in the east and the north. Most roost sites are found in the coastal lowlands (P. A. Racey *et al.*, in litt.).

Although some fragments of littoral forest can be found along the north-eastern coastline of Madagascar, most of it is situated in the south-east. In this report we concentrate on this south-eastern region and more in particular on the littoral forest of Sainte Luce. This type of forest has been considerably reduced in size over time (Ramanamanjato, 2000). Between 1950 and 1995, 3,400 ha, almost half of what was present in 1950, has disappeared. This represents a deforestation rate of 760 ha every 10 years (Mir Télédétection Inc., 1998). At present only highly degraded forest remnants and very few intact forest fragments remain.

In Sainte Luce a colony of 300–350 individuals of *P. rufus* inhabits the littoral forest fragment ‘S6’ (225 ha; Lewis

Environmental Consultants, 1992*b*). This colony has been located there for at least 10 years and according to the local people even longer. These bats are very easily disturbed when approached as a consequence of severe hunting pressure and frequent bush fires in the area (A. Bollen, pers. obser.). Currently there are at least two other roost sites of flying foxes in the region. The largest one contains 800–1,000 individuals and is found in a private reserve, Berenty (25°00'S, 46°18'E; J.-B. Ramanamanjato, pers. comm.). In this gallery forest the bats are more or less protected from hunting. Another roost site is found in a sacred forest 'Enato Anandrano' (24°55'S, 47°00'E) where the bats are protected by the local 'fady', a Malagasy taboo related to the presence of tombs of the ancestors (J.-B. Ramanamanjato, pers. comm.). There is no information on the colony size here and its status as it is forbidden to enter these forests. In the lowland Anosyennes, up north of Sainte Luce, in Marovony (24°05'S, 47°20'E) and Analalava (24°13'S, 47°19'E), two small roost sites, with less than 50 individuals each, were observed in isolated forest remnants (Lewis Environmental Consultants, 1992*b*). Nevertheless, the current status of both bat populations and forest fragments is unknown.

Due to the high degree of fragmentation and degradation of the littoral forest, long distance seed dispersal is important to ensure genetic exchange between plant communities of different forest fragments. At present not much information is available on the diet of *P. rufus* in these littoral forests. Therefore, the main goal of this research is to investigate whether they act as important seed dispersers in this ecosystem by determining which plant species are eaten by these flying foxes. This study forms part of an extensive ecological research project on the mutual dependence of the frugivorous-granivorous guild and the littoral forest flora, more in particular on seed dispersal and predation. Because of this, the focus of this study is on frugivory only and not on nectarivory, and pollen analyses were not carried out.

Materials and Methods

Research Site and Study Period

The littoral forest of Sainte Luce is located in SE Madagascar (24°45'S, 47°11'E) and is considered to be dense humid evergreen forest (Koechlin *et al.*, 1974). It corresponds to the same forest type as mountain rain forest but grows on sandy soils and is always found within 2–3 km of the coast at an altitude of 0–20 m (Lewis Environmental Consultants, 1992*a*). Field research was conducted by the first author between November 1999 and February 2001. During this research period annual precipitation was 2,487 mm with a mean temperature of 23°C, ranging between 12 and 33°C.

The forest fragments of Sainte Luce are considered the least degraded of all. In 1991 they represented a total area of about 1,947 ha. A group of 20 fragments can be distinguished, separated by plains of grassland and swamps. The five larger fragments (incl. S6) range in size from 190 to 377 ha (Lewis Environmental Consultants, 1992*a*). Distances between these five fragments vary from 1.5 to 5 km. Most of them have been separated from each other at least since 1950 and have since then systematically declined in size due to human impact on the edges (Lewis Environmental Consultants, 1992*a*). Today three of them are further degrading by recent 'tavy' (slash and burn followed by cultivation), bushfires, and selective logging.

Fruit Diet: Faecal Analyses and Observations

Most of our data on the fruit diet of *P. rufus* was obtained by collecting and analysing faecal samples. From January 2000 till January 2001 the day roost of the *P. rufus* colony in S6 was visited once a week to collect faecal samples under the roost trees. On each visit as many droppings as possible were collected randomly with a minimum number of five droppings containing seeds. These samples were analysed for seed content, seed number per species and seed viability upon returning at the field station. A reference collection of the seeds gathered from several fragments of primary and secondary forest was made. It should contain the majority of fruits available within the littoral forest during our study period. This reference collection was used to identify the seed species during faecal analyses. For several *Ficus* spp., seeds were too similar to allow identification at species level. For these species identifications were based on the characteristics of the seedlings.

Observations on feeding behaviour were obtained by AB during tree watches and during opportunistic encounters with flying foxes. Because of the difficulty of approaching flying foxes at night these data are limited. The following parameters were scored: visitation length, defined as the time elapsing between arrival of the first bat until departure of the last one in the feeding tree, number of individuals feeding and if possible feeding behaviour. Ejecta pellets collected under the tree were described by their characteristic feeding marks.

Food Selection: Fruit and Seed Characterisation

The following characteristics of fruits and seeds were noted for a total number of 175 individual plant species available in the forest throughout our research period: growth form, fruit type, external colour at ripeness, odour, pulp type, fruit and seed length and mass, number of seeds per fruit, water content and fruit skin thickness. Large trees (> 6 m in height), small trees (< 6 m), shrubs, vines, herbs and epiphytes were the different growth forms considered. Fruit type definitions according to Lambert and Garber (1998) were followed and further lumped into the categories berries, drupes, synconia, capsules and others. External fruit colour could be green, yellow, orange, red or pink, blue or purple, brown, black, white and grey. Odour was scored as absent, present or strong. Pulp type could be juicy or arillate pulp, fibrous pulp or pulpless. Fruit and seed length and mass were measured with callipers and an electronic scale 'Kernbalans NM60' with 0.01 mm and 0.01 g precision, respectively. These measures along with the number of seeds were each subdivided in three classes. The water content of the fruits was calculated by comparing fresh mass and dry mass, after three days of drying in an oven. The fruit skin thickness was divided into the following categories: easily cut by fingernail, by a knife or by a secateur.

We used χ^2-analyses to compare the bats' food selection with the overall fruit availability. A herbarium of all fruit species collected during our study was made in the field and identified by Dr. J. Rabenantoandro at Missouri Botanical Garden in Antananarivo.

Germination Trials

The seed viability after passage through the digestive tract was tested by simple germination trials, in which three different treatments were used; defecated seeds, control seeds and control fruits. Ripe control seeds and fruits were collected on or under the parent plant within a restricted time frame. All seeds were sown at 1 cm depth in plastic pots filled with 8 cm sterile sand and a 1.5 cm humus layer on top. Pots were placed under a shed for protection from direct sunlight. The faecal seeds were still surrounded by their faecal matrix, when sown. For each treatment sowing was done at the same time and under the same overall ecological conditions in order to standardize procedures. The germination rate, defined as time to first germination, and percentage germinated seeds were scored weekly over a period of at least 6 months.

RESULTS

Fruit Diet: Faecal Analyses and Observations

Over a 13-month period at least 40 fruit species (28 genera, 21 families) were consumed by *P. rufus* (Table 1). The bats were observed to eat six fruit species while evidence of 38 species was found in the faecal samples. Eight species were identified as eaten by bats based on the marks on the ejecta pellets found under fruit trees. At least five seed species remained unidentified in the faecal samples and therefore are not shown in Table 1. The family Rubiaceae, including genera *Canthium, Rothmannia, Tricalysia, Canephora, Mapouria, Ixora, Psychotria* and one unidentified genus, was predominant, representing eight fruit species and thus 20% of the plant species in the diet of the bats. Of the remaining 20 families, 11 were represented by only one species, six by two species, and three by three species. The cumulative distribution curve shows that at the end of the 12-month

TABLE 1. Overview of the fruit species consumed by *Pteropus rufus* with indication of plant family, species or gender name and vernacular name, type of evidence (O: observation; F: faecal analyses, M: feeding marks), growth form, fruit type, colour at ripeness, odour (S: strong; P: present; A: absent), pulp type, fruit length (mm) and mass (g), seed length (mm) and mass (g), number of seeds per fruit, and water content (%). Fruit skin thickness was identical for all taxa (easily opened by nail) except for *Rothmannia mandenensis* (by knife only)

Family	Taxon	Vernacular name	Evidence	Growth form	Fruit type	Colour	Odour	Pulp type	Fruit lenght	Fruit mass	Seed lenght	Seed mass	Seed number	Water content
Agavaceae	*Dracaena reflexa* var. *nervosa*	falinandro	F	small tree/shrub	berry	orange	S	soft & juicy	9.1	0.5	5.7	0.1	1–2–3	82
	D. r. var. *nervosa*[1]	tavolobotroka	F	small tree/shrub	berry	orange	S	soft & juicy	15.5	0.9	5.8	0.1	(1)–2–3	88
Anonaceae	*Polyalthia madagascariensis*	fotsivavo	F	large tree	berry	orange	A	soft & juicy	12.2	0.3	7.8	0.1	1	72
Araliaceae	*Polyscias* sp.	voatsilana	F	large tree	drupe	green	A	juicy & hard	5.0	0.0	3.6	<0.01	1	73
Arecaceae	*Dypsis prestoniana*	boakabe	OFM	large tree	berry	orange	P	soft & juicy	14.9	0.6	12.9	0.3	1	80
	D. nodifera	raotry	MF	small tree/shrub	berry	yellow	A	soft & juicy	9.7	0.3	8.3	0.1	1	72
Bignoniaceae	*Ophiocolea delphinensis*	akondronala	M	small tree/shrub	berry	purple	S	soft & juicy	192.9	–	7.6	0.2	150+	74
Canellaceae	*Cinnamosma madagascariensis namoronensis*	vahabatra	F	large tree	berry	brown	S	arillate	22.0	6.2	8.4	0.1	3–13	79
Chlaenaceae	*Sarcolaena multiflora*	meramaintso	F	large tree	capsule	green	A	soft & juicy	14.1	0.7	2.7	<0.01	4–6	81
Combretaceae	*Terminalia fatraea*	katrafa	OMF	large tree	drupe	purple	A	juicy & fibrous	13.2	0.4	8.1	0.1	1	76
Ericaceae	*Vaccinium emirnense*	tsilantria	F	small tree/shrub	berry	red	A	soft & juicy	11.5	0.8	1.4	<0.01	100+	74
Euuphorbiaceae	*Uapaca ferruginea*	voapaky lahy	OF	large tree	drupe	brown	S	soft & juicy	13.6	1.4	10.7	0.2	3 (4)	81
	U. thouarsii	voapaky lahy ZJ	F	large tree	drupe	brown	S	soft & juicy	12.5	1.7	9.6	0.2	3	83
	U. littoralis	voapaky vavy	OMF	large tree	drupe	brown	S	soft & juicy	23.6	4.9	15.0	0.5	3	78
	Ludia antanosarum	hazofotsy	F	small tree/shrub	berry	red	A	soft & juicy	14.0	1.5	2.8	<0.01	6–8	93
	L. antanosarum[1]	zorafotsy	F	large tree	berry	green	S	soft & juicy	12.5	1.0	3.2	3.0	2–11	62
Flacourtiaceae	*Scolopia orientalis*	zoramena	OF	large tree	berry	purple	S	soft & juicy	10.5	0.5	3.8	0.0	2–4	65
Lauraceae	*Beilschmiedia madagascariensis*	resonzo	M	large tree	drupe	yellow	S	soft & juicy	27.7	8.5	20.1	5.7	1	78
	Ocotea sp.	varongy	F	large tree	berry	green	S	soft & juicy	25.0	1.4	15.3	0.6	1	70
Lauranthaceae	*Bakerella* cf. *clavata*	velomihanto sp1	F	epiphytic	berry	green	A	soft & juicy	15.9	0.7	10.4	0.3	1	69
	B. ambongoensis	velomihanto sp2	F	epiphytic	berry	green	A	soft & juicy	8.0	0.1	4.6	<0.01	1	72
Loganiaceae	*Anthocleista madagascariensis*	lendemibe	F	large tree	berry	yellow	S	juicy & fibrous	18.5	3.6	2.7	<0.01	80	76
	A. longifolia	lendemilahy	F	small tree/shrub	berry	yellow	P	juicy & hard	30.3	5.9	3.4	1.0	50–84	70
Monimiaceae	*Tambourissa purpurea*	ambora	F	small tree/shrub	drupe	red	A	arillate	43.8	54.2	11.3	0.3	15–70	80
	T. purpurea[1]	amboralahy	F	small tree/shrub	drupe	red	A	arillate	17.8	5.6	7.5	0.1	6–12	89
Moraceae	*Ficus baronii*	aviavy	F	large tree	synconia	brown	S	soft & juicy	13.0	1.2	–	<0.01	1000+	72
	F. guatteriaefolia	fihamy	F	large tree	synconia	brown	S	soft & juicy	32.8	14.5	1.6	<0.01	1000+	93
	F. pyrifolia	nonoka	F	large tree	synconia	red	P	arillate	6.3	0.1	1.0	<0.01	1000+	61
Myrtaceae	*Syzigium* sp.	rotry mena	OMF	large tree	berry	purple	P	soft & juicy	9.6	0.5	8.1	0.3	1	86

TABLE 1 Continued

Family	Taxon	Vernacular name	Evidence	Growth form	Fruit type	Colour	Odour	Pulp type	Fruit lenght	Fruit mass	Seed lenght	Seed mass	Seed number	Water content
Rubiaceae	*Canthium* sp.	fantsikaitramainty	F	large tree	drupe	brown	A	soft & juicy	7.8	0.3	6.3	0.1	2	68
	Tricalysia cf. *cryptocalyx*	hazongalala lahy	F	small tree/shrub	berry	red	S	soft & juicy	10.9	0.4	4.9	<0.01	7 (5–6)	76
	Canephora axillaris	hazongalala vavy	F	small tree/shrub	berry	red	P	soft & juicy	11.1	0.5	5.8	0.0	4–5–6	78
	Rothmannia mandenensis	taholagna	F	large tree	berry	brown	S	soft & juicy	40.4	35.3	4.3	0.0	100+	63
	?	tainbarika	F	large tree	berry	brown	S	soft & juicy	15.2	2.1	3.7	<0.01	100+	46
	Ixora sp.	x203	F	small tree/shrub	berry	purple	P	soft & juicy	7.4	0.3	4.7	0.1	1–2	83
	Psychotria aegiloides	x210	F	small tree/shrub	berry	red	A	soft & juicy	7.1	5.1	6.3	0.1	2 (1)	91
	Psychotria sp.	x210a	F	small tree/shrub	berry	red	A	soft & juicy	6.3	0.2	5.0	0.1	2	56
Rutaceae	*Vepris elliotii*	ampoly	F	large tree	drupe	green	S	juicy & fibrous	10.2	0.8	7.5	0.1	4	84
Sapotaceae	*Sideroxylon beguei* var. *saboureaui*	ambirimbarika	MF	large tree	berry	green	A	arillate	28.2	3.9	6.6	0.0	7–30	53
Saxifragaceae	*Brexia* sp.	kambatrikambatri	F	small tree/shrub	drupe	yellow	A	soft & juicy	20.2	1.6	15.1	0.2	1	72

[1] — as indicated by their vernacular name in three cases we found two plant species corresponding to the same scientific name. They could represent different ecotypes of the same species or they might be different species that have no taxonomic names yet. As this is difficult to affirm at the moment we preferred including all vernacular names as separate units in our diet list and the 40 plant species are also treated as separate species throughout this paper

period the curve starts to level out ending in a record of 40 species eaten (Fig. 1). January was sampled the 2nd time after completing a year cycle, which did not result in a higher number of species sampled.

Five particular plant species, *Ficus guatteriaefolia, Syzigium* sp., *Terminalia fatraea, Uapaca thouarsii*, and *U. littoralis* were found to be important food sources for the flying foxes during the study period. This importance was based on the larger number of droppings found containing their seeds, the evidence on ejecta pellets, multiple feeding observations or because these species were eaten for at least four successive months, often much longer (Table 2).

Typically one seed species per dropping was found. Out of the 410 faecal samples collected only four samples had two different species of seeds. No sample contained a larger number of taxa. Twenty-three plant species (61%), from a total of 38 food species identified by faecal samples, were represented only by one or two seeds per dropping. More than 50 seeds per dropping were found for 13% of the food plant species. The remaining 26% of the plant species had 2–8 seeds in droppings.

Most of the direct encounters occurred from April through June while the flying foxes were feeding mainly on fruits of *T. fatraea, Dypsis prestoniana* and *Syzigium* sp., and on flowers of *Ravenala madagascariensis*. Out of a total of 47 independent

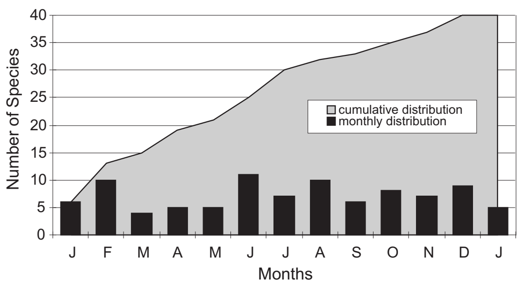

FIG. 1. The monthly and cumulative distribution of the number of plant species eaten by *P. rufus* over a 13-month period

TABLE 2. Temporal distribution of feeding patterns of bats per plant taxon from January 2000 to January 2001 with indication of type of evidence (F: faecal samples; O: observation; S: recognizable feeding signs on ejecta pellets) per month. Number of droppings per taxon is also given. The five most important food taxa are highlighted

Taxon	'Feeding' months													Number of faecal samples	Number of seeds/dropping		
	J	F	M	A	M	J	J	A	S	O	N	D	J		Median	Min	Max
Dracaena reflexa var. *nervosa* 'falinandro'						F								2	1	–	–
D. r. var. *nervosa* 'tavolobotroka'							F	F						4	1	–	–
Polyalthia madagascariensis						F								1	1	–	–
Polyscias sp.										F				2	6	4	8
Dypsis prestoniana					OS					F				1	1	–	–
D. nodifera					SF									1	1	–	–
Ophiocolea delphinensis		S												–	N/A	N/A	N/A
Cinnamosma madagascariensis var. *namoronensis*							F	F	F					11	1	1	3
Sarcolaena multiflora			F											1	9	–	–
Terminalia fatraea				S	OSF	OS	S							3	1	1	3
Vaccinium emirnense		F												1	100+	–	–
Uapaca ferruginea								O	F	OF	OF	F	F	34	1	1	3
U. thouarsii											F			43	2	1	2
U. littoralis							S	F	F	F	F	OF	OF	9	1	1	2
Ludia antanosarum 'hazofotsy'		F				F								2	2.5	1	4
L. antanosarum 'zorafotsy'	F													1	8	–	–
Scolopia orientalis				O				O				OF		1	4	–	–
Beilschmiedia madagascariensis												S		–	N/A	N/A	N/A
Ocotea sp.												F		1	1	–	–
Bakerella cf. *clavata*		F												1	1	–	–
B. ambongoensis				F		F		F						3	9	2	11
Anthocleista madagascariensis											F	F	F	36	50+	27	50+
A. longifolia	F	F												4	4	1	30
Tambourissa purpurea 'ambora'						F								1	1	–	–
T. purpurea 'amboralahy'						F								1	1	–	–
Ficus baronii	F													12	100+	–	–
F. guatteriaefolia	F	F	F	F	F	F	F	F	F	F	F	F	F	148	100+	5	300+
F. pyrifolia										F				25	100+	–	–
***Syzigium* sp.**					OSF	OF	F	F	F	F	F	F	F	44	1	1	2

TABLE 2. Continued

Taxon	'Feeding' months													Number of faecal samples	Number of seeds/dropping		
	J	F	M	A	M	J	J	A	S	O	N	D	J		Median	Min	Max
Canthium sp.									F	F	F			10	2	1	4
Tricalysia cf. *cryptocalyx*	F													1	1	–	–
Canephora axillaries		F												1	1	–	–
Rothmannia mandenensis	F	F	F			F								5	1	1	7
Tainbarika		F				F								1	2	–	–
Ixora sp.							F	F						4	1	1	2
Psychotria aegiloides				F										1	1	–	–
Psychotria sp.								F						1	1	–	–
Vepris elliotii			F											1	5	5	5
Sideroxylon beguei var. *saboureaui*		SF												3	1	3	1
Brexia sp.												F		1	1	–	–

observations (Table 3), the median number of individuals feeding together was 1 (range 1–15) and the median visitation length was 2 minutes (range 1–48 min). Sometimes feeding animals would take off carrying one or more fruits to a neighboring tree, eat them and then return to the original fruit tree. On other occasions individuals would remain eating in the fruit tree itself. The longest visitation length (48 min) and largest group size (n = 15) were recorded in *T. fatraea*. During observations it was also clear from the falling seeds and ejecta pellets that bats most often only suck out juices from the pulp and then systematically drop or spit out the remaining pulp fraction and seeds. This feeding behaviour was noticed for *T. fatraea, D. prestoniana*, and *Syzigium* sp.

Only few data of feeding on flowers were recorded. On one occasion flower petals of *Ludia antanosarum* (Flacourtiaceae) were noticed to be abundantly present in the faecal samples during May while this tree species is blooming. Furthermore the bats were observed feeding on the nectar of *R. madagascariensis* (Strelitziaceae) flying from one tree to another on several occasions.

Food Selection: Exploited Versus Available Food Items

In order to gain some insight into the bats' food selection, the different variables of several fruit and seed parameters were compared for the 175 available and 40 exploited food species (Table 4). Focusing on exploited food species only, it was apparent that mainly large trees and to a lesser extent small trees and shrubs are exploited for their fruits. No herbs and vines occur in the diet list. Berries are the fruit type most represented in the diet followed by drupes. Fruits with a strong odour are predominant in the diet, while all colours are present in approximately similar percentages. Fruits with many tiny seeds as well as one- to two-seeded fruits are well represented. In general, fruit skin thickness is minimal and most fruits have a water content over 60%. Furthermore juicy fruits with a length between 10 and 30 mm are most common in the list, but no particular fruit mass was dominating. Seed length is often smaller than 10 mm and seed mass less than 0.1 g. The threshold for seed swallowing at our study site is as much as 10 mm, with 4.4 mm being the median diameter (n = 38).

Much of the differential use of fruits can be explained by a differential availability. There is only a significant difference between observed and expected values for the parameters pulp type, seed length and seed mass (Table 4). Fruits with juicy pulp are clearly preferred. Fibrous fruits and fruits without pulp, even though available, are not consumed by the bats at all. Fruits with seed length smaller than 10 mm are preferred to longer seeded-fruits. The most preferred seed mass is under 0.1 g, but the 0.1–1.0 g category still makes up one third of their food choice, while seeds heavier than 1 g seem to be avoided.

Germination Trials

Our faecal analyses show that seeds of at least 38 plant species pass through the digestive tract. Due to the scarcity of simultaneous presence of defecated seeds, control seeds and fruits, it was not always possible to obtain the same number of duplicates or the same number of seeds for all treatments.

None of the defecated seeds looked damaged. Only five species provided enough seeds and fruits at the same time to start a germination experiment (Table 5). Passage through the digestive tract had neither negative nor positive impact on the germination rate and percentage of seeds germinated. It appears that seeds from intact control fruits take more time to germinate than seeds of faecal samples and control seeds. Numbers were too small, however, to allow statistical comparison.

Discussion

Fruit Diet Quantitatively

The diet of *P. rufus* studied at Sainte Luce consists of 40 endemic plant species of the littoral forest. Even though our data set represents the most complete information available on the fruit diet of *P. rufus* in littoral forests today, it is probably an underestimation of their overall fruit diet for several reasons. First, by focusing mainly on faecal sample content, larger seeds, that are often spat out and less commonly eaten food species can be missed. Secondly,

Table 3. The number of observations (n) per tree species with indication of the range, median, and average deviation (AD) of the number of individuals feeding in the tree. Visitation lengths (in min.) are also shown

Tree species	n	Number of individuals			Visitation length		
		Range	Median	AD	Range	Median	AD
Dypsis prestoniana	9	1–2	1.00	0.19	1–15	5.0	7.01
Terminalia fatraea	7	1–15	1.00	3.38	1–48	3.0	14.16
Ravenala madagascariensis	5	1	1.00	–	1–2	1.0	0.32
Syzigium sp.	20	1–7	1.00	1.44	1–15	2.5	2.12
Uapaca ferruginea	2	1	1.00	–	1–3	2.0	1.00
U. littoralis	2	1	1.00	–	1–2	2.0	0.50
Scolopia orientalis	2	1	1.00	–	1–3	2.0	1.00
All species together	47	1–15	1.00	1.31	1–48	2.0	5.44

TABLE 4. Comparison of morphological characteristics of fruits (with the corresponding sample size and frequency distribution) in the diet of *P. rufus* (n = 40) and the overall fruits available (n = 152–175)

Fruit parameters	Total fruit availability		Bats' diet		Statistics		
	n	%	*n*	%	χ^2	d.*f*.	*P*
			Growth form				
Larger trees	94	54	23	58	1.42	2	NS
Small trees and shrubs	62	35	15	37			
Others	19	11	2	5			
			Fruit type				
Berry	83	50	25	63	4.64	3	NS
Drupe	51	30	11	27			
Capsule	21	13	1	2			
Others	12	7	3	8			
			Colour of ripe fruits				
Yellow	22	13	5	13	6.00	6	NS
Orange	10	6	4	10			
Red, pink	29	17	9	23			
Purple, blue	16	9	5	13			
Brown	44	25	9	23			
Green	39	22	8	20			
Others	14	8	0	0			
			Fruit odour				
Absent	59	35	16	39	3.30	2	NS
Present	47	28	6	15			
Strong	63	37	18	44			
			Pulp type				
Juicy	124	72	35	88	12.56	3	<0.01
Fibrous	9	5	0	0			
No real pulp	29	17	0	0			
Arillus	11	6	5	12			
			Fruit length (mm)				
<10	42	25	10	25	0.80	2	NS
10–30	97	57	25	63			
>30	30	18	5	12			
			Fruit mass (g)				
<1	69	43	20	51	1.08	2	NS
1–10	79	48	16	41			
>10	15	9	4	10			
			Seed length (mm)				
<10	92	57	33	83	10.71	2	<0.01
10–20	51	32	6	15			
>20	18	11	1	2			
			Seed mass (g)				
<0.1	58	38	24	60	10.11	2	<0.01
0.1–1.0	56	37	13	32			
>1.0	38	25	3	8			
			Number of seeds				
1–2	97	56	17	43	5.57	2	NS
2–50	56	32	14	35			
>50	20	11	9	22			
			Water content (%)				
0–60	28	19	3	8	3.44	1	NS
>60	114	81	37	92			
			Fruit skin thickness				
Cut by nail	150	86	39	97	4.30	2	NS
Cut by knife	23	13	1	3			
Cut by secateur	1	1	0	0			

TABLE 5. The number of weeks needed for the first germination and the percentage of germinated seeds for the three treatments: faecal sample, control seeds, and control fruits. The values given here are median, average deviation (AD), and sample size (*n*)

Species	Germination rate									Percentage germinated								
	Feces			Seeds			Fruits			Feces			Seeds			Fruits		
	Median	AD	*n*	Median	AD	*n*	Median	AD	*n*	Median	AD	*n*	Median	AD	*n*	Median	AD	*n*
Ludia antanosarum	2.5	–	1	3.5	0.50	2	7	–	1	25	–	1	62.5	12.50	2	33	–	1
Terminalia fatraea	25	–	1	22	0.88	3	26	1.20	5	60	–	1	30	15.55	3	30	8.00	5
Syzigium sp.	7	–	1	6	0.90	3	10	5.78	3	50	–	1	80	11.11	3	60	13.33	3
Ficus guatteriaefolia[1]	3.5	2.88	8	7	–	1	15.5	2.50	2	16	9	8	–	–	1	–	–	2
Rothmannia mandenensis[2]	8	–	1	23	–	1	–	–	0	50	–	1	40	–	1	–	–	0

[1]—as these seeds are very tiny and numerous it is impossible to know exactly which percentage had germinated in both control seeds and control fruits
[2]—ripe fruits fall apart in small pieces and therefore we could not sow complete control fruits for comparison

exotic species that are neither important nor typical for the littoral forest were omitted from our study. It is likely that the five seed species that could not be identified may represent seeds from such exotic species. They may also be fruit species eaten in other forest types and were as such not present in our reference collection. It cannot be excluded that the mountain rain forest, with a different floral composition (Koechlin *et al*., 1974) lies within the foraging range of the colony studied. Finally, there might also be an important temporal bias since a number of tree species in these littoral forests do not fruit annually but bi-annually or even less often (L. Randrihasipara, pers. comm.; A. Bollen, unpubl. data). One year of sampling is not enough to establish the complete fruit diet of *P. rufus*. Nevertheless, our species accumulation curve indicates that a large proportion of the diet is indeed already known. Long-term studies are needed to further complete the diet list.

Quantitative data on the diet of *P. rufus* in other parts of Madagascar are limited. In the gallery forest of Berenty the diet of *P. rufus* contains only 13 plant species, both flowers and fruits included (E. Long and P. A. Racey, in litt.). This much lower number can probably be best explained by the lower plant diversity of the much drier gallery forest. P. A. Racey *et al.* (in litt.) have studied *P. rufus* for several years at different sites in Madagascar and their data on feeding ecology resulted in a diet list of 38 plant species for *P. rufus* with two thirds of these being fruit resources. Racey and Nicoll (1984) mention a fruit diet of 18 species for *Pteropus seychellensis* in the Seychelles, and Parry-Jones and Augee (1991) found 22 fruit species in the diet of *Pteropus poliocephalus*. An extensive literature survey by Marshall (1983) resulted in a list of 62 plant genera consumed for their fruits by all *Pteropus* spp. (n = 67) together. All these numbers demonstrate that our diet list, including 40 species belonging to 28 genera is quite extensive.

As for the quantitative data of our observations, we believe there may be a bias on the visitation length scored, as flying foxes would fly away when they detected our presence. On the other hand, visitation length could indeed be relatively short because of a particular feeding behaviour of these bats to consume fruits in ‘dining roosts’ and not in the fruit tree itself on some occasions. This behaviour was also observed for other frugivorous flying foxes (Marshall, 1983) and for Neotropical frugivorous bat species (Kalko *et al.*, 1996; Morisson, 1980), even though Kalko *et al.* (1996) mention a rather sedentary feeding mode for afrotropical flying foxes, which could also be observed in Sainte Luce on other occasions.

Taxonomically

Of the five plant species mentioned in the results, *F. guatteriaefolia* (Moraceae) is likely to be the most important one in the diet of *P. rufus.* This species is available year round due to intraspecific asynchrony in flowering and fruiting and faecal analyses show it was consumed the whole year. It forms a staple food and is likely to be a keystone resource (definition according to Mills *et al.*, 1993) for these bats. *Ficus* spp. are also the food taxon that is most frequently regarded as important in literature on the diet of the flying foxes (Pteropodidae) in the Palaeotropics (Cheke and Dahl, 1981; Marshall, 1983; Fujita and Tuttle, 1991; Banack, 1998) and of fruit bats (Phyllostomatidae) in the Neotropics (Heithaus *et al.*, 1975; Fleming *et al.*, 1977; Morrison, 1980; Kalko *et al.*, 1996).

By the same token, *Syzigium* sp. (Myrtaceae) could be considered a keystone fruit species as well. It is a very common and widespread tree species, which provides food from May up to January. The fruiting cycle of an individual tree is only about two to three months long but since the fruiting pattern in the different forest fragments shows a delay of a few months, the fruits are available in the area for as long as nine months. In this way certain plant species are accessible only to flying frugivores for extended periods.

Terminalia fatraea (Combretaceae) is a highly preferred food item and one of the plant species of which most observations were recorded and large amounts of macerated fruit pulp were found under the trees in the morning. From April to July *T. fatraea* is eaten in very large quantities. There may be a parallel between *T. catappa* consumed in the Masoala Peninsula (Hutcheon, 1994) and *T. fatraea* eaten in Sainte Luce. Both act as important food species during times of fruit scarcity and therefore play a crucial role in the diet of *P. rufus*. *Terminalia catappa* has also been regarded as an important food species for *Pteropus* spp. by Cheke and Dahl (1981), Fujita and Tuttle (1991), and Banack (1998).

Several authors mention that fruit bats feed on a taxonomically non-random subset of fruits. These so-called ‘bat fruits’ are mainly plant species of following plant families: Moraceae, Myrtaceae, Sapotaceae, Arecaceae, Piperceae, Solanaceae, Anacardiaceae, Guttiferae, Leguminosae, and Combretaceae (Marshall, 1983; Fleming, 1987; Banack, 1998; Corlett, 1998). Our data set contains several of these families. Surprisingly the family Rubiaceae, not mentioned by any author, is taxonomically represented by the highest species number in our diet list. On the contrary, Guttiferae and Anacardiaceae, both considered ‘bat families’ by Corlett (1998) and Marshall (1983), are not eaten by *P. rufus* in Sainte Luce even though available. Certain plant families might indeed be considered ‘bat families’ but the actual diet may still vary greatly according to forest type and fruit availability within.

Food Selection

Growth form

A closer look at fruit characteristics for both eaten and available species seems to point at certain food preferences, although at the same time other, non significant, results were rather unexpected. For example the bats did not prefer to eat in large trees. This result was not expected as bats were most often observed and supposed to feed in large trees (Fleming et al., 1987). The often larger fruit crop available at the same time in large trees, the more accessible position and the more easily detectable resources both for bats and researchers are probably responsible for this result. All important food resources in our diet list involve large trees, but shrubs and smaller trees still account for almost 40%. The latter occur in larger numbers in secondary forest and are more easily detected and eaten there. Old World pteropodids are known to be primarily canopy feeders (Fleming et al., 1987) and prefer primary forest to secondary forest (Banack, 1998). In our data set most of the fruit species eaten grow in intact and primary forest. Both pioneer plant species as well as species from a later successive phase were exploited.

Fruit type versus pulp type and water content

The bats eat mainly juicy berries with a high water content. Observations, ejecta pellets, and literature (Marshall, 1983) confirm that fruit juices dominate the diet of flying foxes. As indicated in Table 4, only for the parameter 'pulp type' a significant difference was found between eaten and available fruits, not for fruit type and water content, but these parameters are often intercorrelated. In most tropical forests 50–90% of the plant species depend on animals for their dispersal (Howe and Smallwood, 1982; Fleming *et al.*, 1987) and among typical endozoochorous fruits, juicy berries with a high water content form a large proportion, which stands also for the majority of available fruits in the humid littoral forest of Sainte Luce.

Odour and colour

Most fruits eaten have an odour and even a strong one, which can be related to the bats' well-developed olfactory senses especially used for locating food (Marshall, 1983; Kalko *et al.*, 1996). Odour was a feature of most (65%) of the fruits available in the forest which may explain why analyses revealed that there was no significant preference for this trait. This abundance of odorous fruits is probably because a large amount of the available fruit species are dependant on mammals for seed dispersal and scent in general is also of major importance for mammals when locating and selecting ripe fruits. Besides good smell, the flying foxes have also developed large eyes and thus good vision which might further help them to locate fruits at night (Marshall, 1983). Obviously colour is of little relevance since they feed and forage at night and all nocturnal mammals are colour-blind (Corlett, 1998). This is confirmed by the fact that selection of fruits in favour of a particular colour was not observed.

Size versus mass

Based on the number of seeds per dropping we presumed that tiny seeds of multiseeded fruits with a length up to 1–3.5 mm are likely to be automatically swallowed together with the fruit pulp. As for larger 1- to 2-seeded fruits, with seed length between 3.5–20 mm, fruit skin and seeds are most often spat out. This feeding behaviour of dropping larger seeds and swallowing tiny seeds together with fruit juices was also mentioned by Marshall (1983). Occasionally some seeds (up to 15 mm length) are swallowed as well. For all three *Uapaca* spp., with seed length over 9.6 mm, seeds were often swallowed but this is probably due to the pulp texture and seed slipperiness. The threshold for swallowing seeds is reported as being less than 3.2 mm diameter for a 600 g *Pteropus* sp. and between 3–5 mm for flying foxes in general (Corlett, 1998; Shilton *et al*., 1999), which is smaller than 10 mm recorded at our study site.

Our analyses showed no particular fruit mass preferences. The fact that *Pteropus* spp. may transport fruits of over 200 g (Marshall, 1983) means that they are probably not limited by masses up to 50 g, being the maximum fruit mass that was scored.

'Bat fruits'

According to Fleming (1979), Marshall (1983), Stashko and Dinerstein (1988), Thomas (1988), and Korine *et al.* (1998) 'bat fruits' can be morphologically characterized as variable in size with a green or dull colour, a strong and musty odour, high water content, pendant position or held away from the foliage. This description corresponds with our results meaning that the bats' food species in Sainte Luce include fruits of all size, having no particular conspicuous colour, a strong odour and high water content. However, compared to the overall database of available fruits in this forest several of these variables are simply characteristic for the majority of fruits. Thus real food selection or clear preference cannot be established. Therefore it is important that future studies also focus more on all available food resources in an ecosystem rather than studying the diet of the bat species only. This way it will be possible to draw broader conclusions on real food preferences and typical 'bat fruits' compared to the wide array of fruits available.

The Exclusive Role of Flying Foxes in Seed Dispersal

Quantitatively important short and long distance seed dispersal

Pteropus rufus feeds on a huge variety of fruits, which makes this species potentially an important seed disperser for a large number and diverse set of endemic plant species in the littoral forest. Compared to other frugivores in the littoral forest it is the only one capable of long distance seed dispersal since foraging may occur up to 50 km away from the roost site (Thomas, 1988) thereby bridging isolated forest fragments. This ensures genetic exchange between plant populations of different forest fragments, and for very small fragments no longer inhabited by other mammal seed dispersers, only bats can disperse these fruits. Long distance seed dispersal happens mainly between successive feeding trees (0.3–8.3 km apart) or even further away between foraging areas and roost sites (up to 50 km apart) for all ingested seeds (Morrison, 1978; Korine *et al*., 1999).

Gut passage rate in flying foxes is often only about 30 minutes (Morrison, 1980), although there is also evidence for gut retention of food for longer (> 12 hrs or even >18 hrs) periods (Shilton *et al*., 1999), which increases the possibility for long distance seed dispersal. As digestion can be rapid, large quantities of food can be processed every night. This is necessary because being flying mammals, these bats have rather high-energy requirements and may eat at least the equivalent of their own body mass each night (Marshall, 1983; Shilton *et al*., 1999). In addition, they are very numerous in the area. All this probably leads to a massive consumption of fruits and possible dispersal of seeds every night by a large number of animals.

Germination experiments

Izhaki (1995) noted a positive effect of passage through bats' guts on germination rate of the ingested seeds. Nevertheless, Palmeirim *et al.* (1989), Kalko *et al*. (1996), Iudica and Bonaccorso (1997), Korine *et al.* (1998), Shilton *et al.* (1999) as well as this study did not find such a relation. There was no positive or negative impact on germination rate and germination percentage of defecated seeds. The results on percentage of plants that finally germinated after six months are difficult to interpret and appear very variable. More extensive experiments under more controlled ecological conditions and with more replicas should be carried out to confirm these first preliminary data. But, even if germination itself does not profit from the digestive process, more important to consider is the distance covered by the flying foxes during gut passage.

Threats and Conservation Options

Unfortunately in Sainte Luce not only the fragmented habitat is at risk, but its inhabitants among which the flying foxes, are seriously threatened as well. During our field research the whole colony moved once from their original roost site to another one, five kilometers west, where they remained from February through May 2000. Afterwards the colony returned to the first roost site. At both roost sites, rocks, long sticks and injured patagia were indications of severe hunting pressure. Several bush fires in the nearby area perturbed the colony even more. Too much harassment might cause the colony to divide into smaller groups, and settle elsewhere, leaving the littoral forest deprived of its only capable long distance seed disperser.

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